



INTERNATIONAL JOURNAL OF
**COMPARATIVE
PSYCHOLOGY**

Published by
The International Society
for
Comparative Psychology

VOLUME 10, NUMBER 1

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Volume 10, Number 1, 1997

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Subscription rates:

Volume 10, 1997 (4 issues) \$95.00 (outside the U.S., \$110.00). Members of the International Society for Comparative Psychology receive their yearly subscription as part of their membership dues. For membership information see back pages.

INDEXED OR ABSTRACTED IN: Psychological Abstracts.

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THE LOGIC OF SEARCHES IN YOUNG CHILDREN (*HOMO SAPIENS*) AND TUFTED CAPUCHIN MONKEYS (*CEBUS APELLA*)

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ABSTRACT: Nine young children and five tufted capuchin monkeys (*Cebus apella*) were tested on tasks involving a search for an object hidden within a set of plastic cups. As viewed, the sequences of displacements enabled subjects to eliminate some of the possible locations where the object lay hidden, thereby constraining the search space. Both species deployed principled modes of search, in contrast to a random selection strategy. However, no subject from either group proved able to fully constrain the search on the basis of all of the information conveyed over the full menu of tasks. The reasons for incomplete success are as yet unclear, however failures may be due as much to social limitations as to other forms of error. On that basis we conclude that new paradigms are necessary, designed specifically to evaluate competencies for socially based knowledge on the one hand and self-directed search on the other.

Memory and representation have a long history of exploration in research on both human and non-human species. Perhaps the oldest form is the delayed-response task pioneered by Hunter (1913), elaborated later with primates by Yerkes (1929), and culminating in the well-known versions introduced by Piaget (1955) as "object permanence" tasks. A common feature of these tests is the role they give the tester who first acts to capture the subject's attention by presenting an attractive object, such as a toy, or a piece of preferred food, before hiding it within containers or behind occluding screens which remain at all times within the test field. Either immediately afterwards, or following a delay, the subject is given an opportunity to seek hidden items. Persistence of search in the absence of direct perceptual information is the first indication of object memory or event permanence. However, beyond search oriented behaviour *per se*, the use of strategies may indicate a great deal about the subject's ability to

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constrain search to the relevant container alone, or, in the case of direct information concerning the precise location of the bait, to infer from its absence the most likely locations which remain to be explored.

Thus, infants in an object permanence task may search the first container visited by the experimenter, even though the item sought has been quite explicitly removed and placed in an alternative site by the experimenter, in full view of the subject (Bower, 1974; Diamond, 1985). In tasks, furthermore, where the act of hiding could not be perceived directly, but could be inferred only from the sequence of events in each task, Haake and Somerville (1985) found a strong developmental trend from 9 month to 18 month old infants in the way they co-ordinated temporal and spatial information. As these authors point out, the sequential nature of the hiding procedures required children "to attend to, remember and use information about the presence and absence of the object in the context of movements among potential hiding locations. In order to search logically, events occurring at different times and places in the displacement sequences had to be linked together to determine exactly where the object had been hidden" (page 185). Under these conditions, only the oldest children in the sample showed some consistent search pattern, for example, searching the last place the target object was seen, following a discovery that it was now "missing".

Tests of "pure" cognitive competencies are rare, if they exist at all, however. As in so many other such cases, the task used - or the conditions under which it is introduced - may itself be a factor in determining whether subjects will deploy exhaustive and relatively inefficient strategies or opt instead for controlled, efficient search. Certainly, Wellman, Somerville and Haake (1979) found considerable task-induced differences in strategies (which themselves change with age) of children aged from 2 to 6 years. Given doors in a cupboard to search versus areas of a playground, for example, children's responses indicated that "searches were more systematic and comprehensive in the cupboards than on the playground" (p. 541). The authors account for this difference by suggesting that searching "logically" makes greater demands on limited cognitive resources than other strategies, and that certain environments may be easy to search completely, as their cupboard task indicates. Certainly, this factor has been given further emphasis by the findings of Somerville and Capuani-Shumaker (1984). Their study, which forms the basis of the investigation reported in this paper, found that children from 3-5 years of age were able, under some circumstances at least, to constrain search on the basis of

watching a tester hide or find an object within a small test field containing 4 hiding places. Somerville and Capuani-Shumaker suggest, in fact, that making the children pay particular attention to the task (affording, as it does, a low cost solution even if the subject searches randomly) is a crucial factor in the subjects' success.

Whatever the role of the various factors involved, it is surely clear that the tasks described are of interest to the comparative psychologist, designed as they are both to evaluate the role of observer based and self-directed (discovery based) inference, in promoting search economy in a situation not unlike a foraging task (see McGonigle and Chalmers, 1992). Watching a conspecific visiting putative food sites, for example, may materially reduce the costs of search by an observer otherwise left to its own devices. Left to its own devices, on the other hand, the way an agent searches may also have a profound impact on the effort it expends when achieving its goal. Executing search in a random and unprincipled way, for example, could lead to costly reiterations, especially if the search space and the actual space to be searched is large (see Olton, 1982).

In summary, there would appear to be 2 main aspects to the search problem as described. The first is concerned with the extent to which an agent can improve efficiency of exploration when observing the behaviour of others. The second is concerned with the sorts of strategies which an agent, working on its own, will devise to keep search as efficient as possible. Common to both, are the cost functions which the agent must calculate in deciding if it is worth the effort of devising a strategy designed to make search efficient i.e. the "cost" of inference must be offset by the benefits of search economy. In this report, we seek primarily to determine whether socially transmitted search constraints are exploited by a non-human primate (*Cebus apella*). Since in the developmental studies just cited only percentages of children solving a particular condition of the experiment are reported and it is impossible to unambiguously characterise individual profiles among conditions, and since specific verbal instructions were used in the Somerville and Capuani-Shumaker study (1984) - we decided to first test some children of ages similar to those used in the Wellman et al. (1979) and Somerville & Capuani-Shumaker (1984) investigations. In doing so we modified the tasks where necessary, making them as similar as possible to those designed for the *Cebus apella* - who could not benefit, of course, from linguistically based instruction. In this way, we hoped to establish a robust template of performance in young children (when amalgamated in the research just cited) against which

the non-human primates could be compared.

EXPERIMENT 1: CHILDREN

METHOD

Subjects

The subjects were 9 children (5 boys and 4 girls) with a median age of 4 years and 11 months and a range of 4 years and 8 months to 5 years. All children attended the nursery of the Department of Psychology of the University of Edinburgh.

Apparatus

The testing apparatus was a specially modified WGTA, designed to enable the simultaneous presentation of a maximum of 5 stimuli (McGonigle & Chalmers, 1992). For the test described here, four white plastic cups were presented in line across a 18 x 50 cm tray. The objects to be hidden were a red and a blue rubber eraser which could be enclosed in the tester's hand and placed silently under a given cup, without giving any clues that it had been hidden there.

Procedure

Before each daily session, each child was taken from the departmental nursery to an adjacent testing room. The child sat in front of the tester, in full view of the cups, unless occluded by a screen. Each session lasted approximately 12 minutes. A camera positioned in front of the subject recorded his/her behaviour while looking at the hiding/finding procedure as well as while responding. A hiding and a finding task with relative warm-up trials (described below) were presented to each subject. Five subjects, selected at random (three boys and two girls), were presented first with the hiding task and the remaining four (two boys and two girls) were presented first with the finding task.

Hiding task. At the beginning of each test session, each child was told that the object was going to be hidden under a cup and that their task was to find it by lifting the cups. Before the administration of the hiding task, each testing session featured the presentation of warm-up

trials of two different types: type 1 and type 2. Type 1 warm-up trials were presented in each experimental session until a criterion of two consecutive correct searches, each performed within a latency of 5 sec., was achieved. In each of these trials, the tester's hand was moved under one cup and then removed and opened in order to show that the object was now absent. The subject was then allowed to search under the cups.

The rationale for the presentation of warm up trials type 1 was to assess whether the subjects were able to constrain their searches on the basis of the information provided by the hiding procedure. This was a necessary precondition for the presentation of a longer series of displacements such as that involved in the actual hiding and finding task. After the presentation of the type 1 warm-up trials, two type 2 warm-up trials were presented in each experimental session. In these trials the object was shown in an open hand at one end of the cups array. The hand was then closed and moved under all the four cups in succession, before being opened after the fourth cup to show that the object was now absent. The subject was then allowed to search under the cups. In one trial the hand moved from right to left and in the other trial from left to right.

The rationale for the presentation of the warm up trials type 2, was twofold. On the one hand it would have allowed an assessment of the ability of the subjects to understand that, after a series of displacements the object was still to be found within the array of cups (although in absence of any explicit information about the precise location of it under one particular cup). On the other hand, and because of the circumstance that the subject does not know the precise location of the object, the presentation of these trials would have allowed an evaluation of the way the subjects spontaneously perform an exhaustive search of a set of locations. In more detail it was interesting to evaluate whether, in absence of explicit information about the precise location of an object the subjects would have adopted a Systematic mode of search (i.e. a principled strategy such as searching always from one end to the other of the array), as opposed to an Asystematic mode of search (i.e. searching in a random order one location after the other).

The presentation of the warm-up trials was followed by the presentation of the experimental trials. Each daily session comprised a total of four experimental trials. Two trials conformed to a sequence of displacements referred to as the Object Present (OP) condition. The other two trials conformed to a sequence of displacements described as the Object Absent (OA) condition.

In the Object Present (OP) condition, the object was shown in a open hand at one end of the cups array, the hand was then closed and moved under all the four cups in succession before being opened after the fourth cup to show that the object was now absent. Between the second and the 3rd cup the hand was opened, to show that the object was still present in the hand. This critical event happening between hand's visit to the 3rd and 4th cup therefore allowed the inference that the object had been hidden under either the 3rd or the 4th cup visited. The alternation of the hand's direction of travel (right to left and left to right) assured that the 2 cups under which the object could be were not the same ones in the two trials administered in a daily testing session. A schema of the sequence of movements and events featured in this condition of the hiding task is shown in Figure 1, top left. The figure also illustrates the possible location of the object after a right to left (upper line) and a left to right (lower line) sequence of displacements.

For the Object Absent (OA) condition, the sequence of displacements was identical to that used for the OP condition, except for the fact that, when the hand was opened between the 2nd and 3rd cup, it was shown to be empty. As for the Object Present condition one sequence was left-to-right and the other right-to-left (see Fig. 1 bottom left, upper and lower line).

To summarise, in one experimental session, two trials of both Object Present and Object Absent conditions were administered to each subject. These included the experimenter moving his hand from left to right, and from right to left, for one trial of each condition, for a total of four trial types. The order of presentation of the four trials was selected at random for each daily session. Four daily testing sessions were administered and therefore a total of sixteen trials was collected for each subject.

Finding task. The verbal instruction given to the children at the beginning of each daily session was: "here are two objects which always hide together under the same cup; I will find one of them and you must find the other one". For each trial, a cardboard screen was interposed between tester and subject and the objects (now two, a red and a blue eraser) were hidden under one of the cups, out of the sight of the subject.

As for the hiding task, the administration of the finding task was preceded by the presentation of type 1 warm-up trials (until the achievement of the criterion) followed by two type 2 warm-up trials. These trials were similar to those used for the hiding task. The only

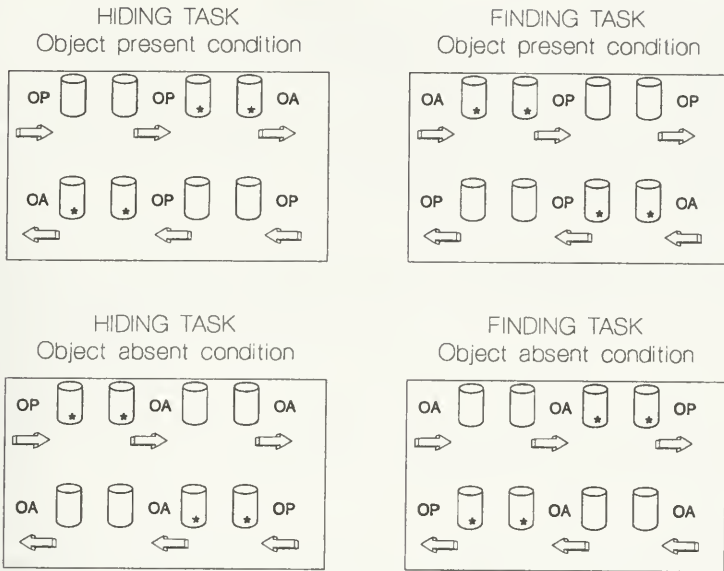


Figure 1. Schema of the Object Present (top) and Object Absent (bottom) featured in the hiding (left) and the finding (right) task. The events shown to the subjects at the beginning of the sequence of displacements, at the end of the sequence of displacements and the critical event shown after the hand had been passed under the 2nd cup and before it was passed under the 3rd cup are also depicted. OP (Object Present), indicates that the object is shown to be present in the tester's hand at that point of the sequence of displacements; OA (Object Absent), indicates that the tester's hand is shown to be empty at that point of the sequence of displacements. Arrows indicate the direction of travel of tester's hand. Asterisks indicate the possible location of the objects after the completion of the hiding/finding procedure.

difference was that the tester's hand was initially shown empty and later, after passing under the cup(s), revealed to contain one of the objects. The rationale for the presentation of both these types of warm-up trials was the same described above for the hiding task.

After the presentation of the warm-up trials four experimental trials were presented in each daily session. These experimental trials were analogous to those given in the hiding task, except that the objects were hidden, initially, out of sight of the subject. The informing event at the beginning of the sequence was now the absence of objects in the tester's hand. The intermediate event between the 2nd and the 3rd cup was either the presence of one of the objects in the tester's hand (OP

condition) or its absence (OA condition). A schema of the four different trials is shown in Fig. 1 (top right and bottom right).

The counterbalancing of the sequences of displacements followed the same schema as described for the hiding task. As for the hiding task, four daily testing sessions were presented and overall a total of 16 trials was collected for each subject.

Data recording. The tester recorded the location and order of occurrence of each search performed by the subject. A search was defined as the lifting of a cup. A scrutiny of the videotape records was performed in slow motion mode, in order to ensure that the data analysis was conducted only on those trials in which the subject watched without interruptions the whole hiding\finding procedure. In the event, none of the trials had to be eliminated.

Statistical analysis. All statistical analyses were based on the Binomial Test. In the Warm-up 1 trials the probability of occurrence of a successful (locating the object) search by chance was $p=.25$. In the hiding and the finding task the probability of performing an appropriate (selecting one of the two locations where the object could "logically" be hidden) first search by chance was $p=.50$, whereas that of locating the object (successful search) by chance in a second search (following an appropriate but unsuccessful first search) was $p=.33$.

RESULTS

Warm-up trials

In Type 1 of the hiding task, all the children understood the hiding procedure, satisfying the criterion of two consecutive correct responses with a latency of <5 sec. The group performance was of 87% correct responses ($p<.01$) and all subjects showed a proportion of correct responses above chance level ($p<.01$).

In the finding task, type 1, all children but one understood the procedure, reaching the criterion of two consecutive correct responses, each performed within 5 sec. The group performance was 45% correct responses ($p<.01$). The individual scores showed that 7 children out of 9 performed a significant ($p<.01$) proportion of correct responses.

In view of the similarity of the warm-up type 2 data from both hiding and finding tasks, these were combined in an analysis of the

different modes of search adopted by the subject to explore the array during type 2 trials. These have been divided into Systematic mode of search, i.e. the subjects explored the array from one end to the other (no fixed sequences other than end to end exploration were observed) and Asystematic mode of search, i.e. the search was performed at random. As should be expected by chance ($p=.25$), in the absence of any clue about where to search, the subjects located the object on their first choice only in the 21% of the trials. Subjects adopted a Systematic mode of search in the remaining 49% of the trials and an Asystematic one in the remaining 30% of the trials).

Hiding and finding task: Group performance

First searches. The percentages of appropriate first searches performed in the hiding and the finding task are shown in Table 1. From these it can be seen that appropriate first searches were performed above chance level. However, the most striking feature of the data is the selective effects of the sub-conditions within each task type. In the hiding task, the OP condition contributes almost uniquely to the overall success within this condition. In the finding task, by contrast, the OA condition is the most successful.

Second searches. As not all searches could be successful on the first choice even when controlled by a logical strategy, it was necessary to analyse second choice behaviour following putatively appropriate if unsuccessful first choices. Thus, second searches have been included in Table 1. In the case of both tasks, second choices (following an appropriate but unsuccessful first choice), are significantly in accordance with the choice of the appropriate location (i.e. locate the object). As Somerville and Capuani-Shumaker (1984) point out, however, it is necessary also to distinguish between endpoint based second choices and mid-position ones. This is because second choices which follow on from a choice of an end location and are adjacent to the endpoint, may be simply the result of object proximity *per se*, and not at all a reflection of the subject's understanding of the implication of the first choice. By contrast, when the first choice is performed at an appropriate inner location, a second response performed on the basis of mere proximity would locate the object only in the 50% of the occasions. For this reason, in Table 1, second searches have been divided into those that followed first searches at inner and end points of the array. It can be seen that subjects were significantly searching in the appropriate location in both tasks, even when only second searches following a first search at an inner point are considered.

Table 1. Distribution of children's searches in the hiding and finding tasks. OP, Percentages of total number of appropriate first searches in the Object Present condition; OA, appropriate first searches in the Object Absent condition; Successful second searches, occasions where the subjects locate the object following an appropriate although unsuccessful first search in which the Object had not been found; FI, The relative contribution to second search success of searches performed following an inner point based first search; FE, searches performed following an endpoint based first search. *, $p < .05$; **, $p < .01$.

Task	Appropriate first searches (%)			First search outcome (%)		Successful second searches (%)		
	All	OP	OA	Object found	Object not found	All	FI	FE
Hiding	74**	89**	58	66	34	88	79**	100**
Finding	68*	61	75**	69	31	75**	67**	84**

Hiding and finding task: Individual performances

Given the asymmetrical distribution of appropriate first searches between the two sub-conditions of the hiding and the finding task and between the two tasks themselves, it is particularly interesting to consider how each child handled the various situations. A probability of 0.05 or less obtained on the basis of a binomial test conducted on the percentages of appropriate first searches in each of the conditions of both tasks was considered as evidence of success for a particular subject in a particular condition. Only one child succeeded in both conditions of the hiding task and one in both conditions of the finding task. The behaviour of the remaining subjects is highly consistent with the group results: performing appropriate searches mostly in the easiest condition of each task. No subject searched in the appropriate location in both tasks. Combining the percentages of appropriate first searches performed by each subject in the two conditions of each task, it emerges that three children searched appropriately in the hiding task and two in the finding task.

Identification of strategic behaviours

Up to this point, we have evaluated how successful our subjects were in selecting the two appropriate locations on the basis of the inferences that could be drawn from the observed sequences of displacements. However, it is important to take as much of the behaviour into account as possible. In fact, some strategies (which do not lead directly to "significant" correct performance) could possibly be identified by an analysis of the whole data base which includes both appropriate and inappropriate responses. The presence of strategies would indicate that searches, even when not appropriate, are not performed at random. In order to evaluate this possibility, we subjected the choice data to a further analysis based on a taxonomy of other strategic possibilities proposed by Somerville and Capuani-Shumaker (1984) and described as follows.

For each subject, a significant difference ($p < .05$) from the value expected if first choices oscillated randomly between two possible pairs of locations (Binomial Test, two tailed) was considered as evidence for conformity to a strategy.

One strategy would lead to a bias towards the selection of either the first two or the last two locations visited by the tester's hand and can be designated as temporal. Two children conformed to a temporal strategy in the hiding task and one in the finding task, selecting consistently the last two locations.

Another strategy could be a simple position bias toward the two left hand side (LHS) or the two right hand side (RHS) locations. In the hiding task, one subject conformed to this spatial strategy selecting consistently the right hand side locations, while in the finding task such a strategy was used by two subjects: one selected the right hand side locations and the other one chose the left hand side locations. Overall, only two subjects did not appear to use any strategy at all in the hiding task and three in the finding task.

To examine strategic consistency, the relationships between the strategic behaviour of each subject on each of the tasks, was evaluated. There was little evidence that strategies deployed in one task were used by the same subject in the other. For example, two of the three subjects that showed evidence for a "logical" strategy in the hiding task did not conform to any strategy in the finding task and the third, in the finding task, always chose the last cup visited by the tester. The two children that selected the appropriate locations in the finding task, always selected the same location or did not using any strategy at all, when presented with the hiding task. Ko searched according to a temporal

strategy (Last 2) in the hiding task and according to a spatial strategy in the finding task (RHS). Br did not use any strategy in the hiding task but conformed to a spatial strategy in the finding task (LHS). Gi did not conform to any strategy in both the tasks and An, who was tested in the hiding task only, searched according to a spatial strategy (Last 2).

DISCUSSION

Children in this study are not found fully competent to use observationally based constraints on choice when both hiding and finding tasks are taken as criterial. No child succeeded in both tasks. Instead, success was partial, emerging primarily in the Present Condition of the hiding task, and the Absent Condition of the finding task. A similar trend has been found by Somerville and Capuani-Shumaker (1984). This result, combined with our evidence that the behaviour, even when inappropriate, was essentially non-random indicates that the children's failure was not merely the result of boredom, or of inappropriate testing procedures. Overall the picture which emerges from the child data appears a heterogeneous one. Some children seem to perform observationally constrained searches in one or the other of the two tasks. However, no one subject conforms fully to the criteria set to determine "logical" search in both tasks and for both conditions of each task. There are, nevertheless, many consistent features of performance which suggest that data are not idiosyncratically generated by each subject, nor the product of poor test conditions or procedures. Instead, we would argue that, this suggests that children of the age we tested are only partially competent at dealing with some of the implications of events which they perceive directly, even in a situation as (ostensibly) simple as the one we describe. There is evidence of a difficulty in dealing with information implied by the absence of an object or event. In addition, the requirement to couple simple background knowledge (conveyed linguistically) with the interpretation of directly perceived events is far from optimal. These lacunae aside, however, there is also evidence of a gradient of constraint on search and object choice which these subjects may exploit on the basis of the observations of the behaviour of a third party. Would this also be true of the behaviour of a non-human primate, the *Cebus apella*? We addressed this question in our next study.

EXPERIMENT 2: MONKEY - PHASE A

The experiment with the monkeys comprised two different phases, phase A and phase B. A precondition for the administration of the hiding and finding tasks which feature complex sequences of displacements is that the subject will search at all, under conditions where the size of the set to be searched is four items and sometimes under delays of at least 3 sec. Phase A was essentially an attempt to give the monkeys experience of searching under these conditions. Phase B featured the presentation of the hiding and the finding task to the monkeys.

METHOD

Subjects

The subjects were two adult males (Al and Ch) and three adult females (Lu, Ki and Ol) wild born tufted capuchin monkeys (*Cebus apella*). They were housed in a colony compound within the Laboratory for Cognitive Neuroscience of the University of Edinburgh. At the time of the experiments the colony was composed of two adult males and five adult females. The enclosure was equipped with perches, water sources, tree branches and hangers suspended from the ceiling in order to provide locomotor opportunities. A layer of wood shavings covered the floor. To encourage foraging behaviour, a mixture of seeds was dispersed into the wood shavings on daily basis. Water was available *ad libitum*. The monkeys were transferred in individual cages for the testing sessions that took place in the morning. Reward was based on highly preferred food (grapes). All the monkeys were experimentally naive and had just terminated a period of quarantine of 6 months.

Apparatus

The testing apparatus was analogous to the modified version of WGTA, used for the children in experiment 1. The cups used to cover the bait were the same sort of white cups used for the children in experiment 1. The bait was a white grape that could be enclosed in the tester's hand and placed silently under the cups without giving the subject any auditory or visual clue. Up to 5 polystyrene white cups were used to cover the objects.

Procedure

Essentially this phase of the experiment was motivated to enable the monkeys to cope with up to 5 cups per trial and a delay interposed between hiding and retrieval. To achieve this, 3 conditions were presented to the monkeys in the following order: a visible baiting condition, comprising 5 phases featuring the presentation of 1, 2, 3, 4 and 5 cups, respectively; a control condition; and a delay condition. The data recording was as described for Experiment 1.

Visible baiting condition. A cup was baited while the subject was looking. Starting from trials in which only one cup was presented on the tray, the number of cups was increased until a linear array of five cups was presented. For each trial, the cup to be baited was randomly chosen within the array. When the subject reached a criterion of five consecutive correct responses, each performed within a latency of five seconds, one more cup was added to the previous array. On reaching this criterion for the five cups array, subjects were overtrained for several sessions to ensure a stable performance before the administration of the next stage.

Control condition. An array of 5 cups was presented. The procedure consisted in moving a second cup simultaneously with the displacement of the bait. Thus the mere movement of a cup could not be taken as a sign indicating which cup was being baited. The second cup to be moved was randomly selected for each trial.

Delay condition. The task featured the presentation of a 5 cups array. First, a 3 sec. delay was introduced between the displacement and the retrieval of the bait, subsequently increased to 5 sec., for those subjects which did not show a noticeable performance decrement.

Statistical analysis

A Binomial Test was performed on data obtained from the extensive testing with the 5 cups array, the Visible Baiting Condition, the Control Condition and the Delay Condition. The probability of occurrence of a successful search by chance was $p=.20$.

RESULTS

Visible baiting condition. All subjects immediately searched for the bait when it was hidden under the only cup presented. In the phases

featuring the presentation of 2, 3, 4 and 5 cups, the averaged numbers of trials to criterion were 24.6 ($sd=20.9$), 8.6 ($sd=4.1$), 8.8 ($sd=4.1$), 6.8 ($sd=2.2$), respectively. The highest number of trials to criterion was found (for four subjects out of five) in the condition where two cups were presented. For one subject (Lu) the highest number of trials to criterion was found when it was presented with 4 cups. The averaged percentage of correct choices in the extensive testing with the five cups array was 92.8% ($sd=4.4$, $p<.01$). The overall percentage of correct choices made by each subject was also highly significant (Al=97%, $p<.01$; Ch=91% $p<.01$; KI=94% $p<.01$; Lu=96% $p<.01$; O=86% $p<.01$).

Control condition. The mean percentage of correct choice in the control condition was 90% ($sd=9.5$), $p<.01$). All the subjects showed a highly significant percentage of correct responses. Only one subject (Ki) showed, in this condition, a percentage of correct responses lower than that shown in the previous test phase (visible baiting condition with five cups).

Delay condition. The interposition of a 3 sec. delay between hiding and retrieval did not disrupt the performance of 4 subjects out of 5. The percentages of correct choices made by Ol (90%), Ch (94%), Lu (80%) and Al (92%) were all highly significant, while that performed by Ki (32%) did not reach statistical significance. When the delay was increased from 3 to 5 sec. most subjects expressed distress by either staying apathetically in a corner of the cage without paying attention to the testing procedure or by moving frantically and occasionally shaking the apparatus. We were thus obliged to terminate the administration of this condition. However, the two subjects (Ol and Ch) that received enough trials to compare their percentages of correct responses (Ol=68% and Ch=73%) to chance, searched correctly ($p<.01$) even when a 5 sec. delay was interposed between hiding and retrieval.

DISCUSSION

Visible baiting condition. Results obtained from this first set of tests show that all subjects were committed to search for an object they had seen disappear under a cup. The incentive to search for an object, now out of sight, was apparent even from the first condition in which only one cup was presented. However, in a single cup condition, the action of lifting it might be expression only of a manipulative disposition on the part of the subject, and not necessarily motivated by

the bait *per se*. The fact that the subjects chose the baited cup only, under multiple cup conditions, indicates to the contrary. Nevertheless, this selective response in the presence of multiple hiding places was acquired in the course of testing and was not expressed spontaneously. It would seem, therefore, that there is already a disposition to use a self-directed mode of search. When one cup is presented, this mode is sufficient for immediate success; where there are alternatives, however, it is not. Informed by failure, however, the monkey's search, once constrained through observation of the tester, appears unaffected by the addition of further distractors (up to five cups presented in a linear array).

Control condition. Results obtained from the control condition show that subjects were not using cup movement alone as a unique clue to location of reward. Instead, the serial displacement procedure alone was taken as the informing event.

Delay condition. An evaluation of the delay that subjects were able to tolerate was necessary before Phase B of Experiment 2; that required an attentional phase of approximately 2-3 sec., if the tasks were to be administered successfully. As four of the subjects proved able to cope with an interval of at least 3 sec. a necessary precondition for Phase B was satisfied.

EXPERIMENT 3: MONKEYS - PHASE B

METHOD

Subjects

The four monkeys (Al, Ch, Lu, and Ol) that proved able to tolerate at least a 3 sec. delay in the preceding stage were used as subjects in this phase.

Apparatus

The testing apparatus was the WGTA used for Phase A. Four cups, identical to those used in Experiment 1 and in Phase A of experiment 2, served to cover the baits. The baits were black and white grapes.

Procedure

The administration of the Warm-up trials and the experimental

trials of the hiding and finding task to the monkeys was as described for children in Experiment 1. Two monkeys (Ch and Lu) were first presented with the hiding task and the remaining two (Al and Ol) began with the finding task.

Warm up. The warm up trials presented to the monkeys, both for the hiding and the finding task, were identical to those presented to the children and described for Experiment 1.

The procedure adopted with the monkeys in the hiding and the finding task followed the same schema featured in Figure 2, with the following minor modifications.

Hiding task. At the beginning of each daily session subjects were motivated with five trials in which the bait was hidden under a cup and the subject had to retrieve it. This was followed by 4 experimental trials.

Finding task. Before the administration of the finding task, it was necessary to convey, non linguistically to the subjects the crucial information that two baits were always hidden together under the same cup. This was attempted by administering a task identical to the visible baiting condition described above, except for the fact that two baits (a black and a white grape) were hidden together under one of the cups. This was followed by 4 experimental trials per session using the procedures as described for children in Experiment 1.

Statistical Analysis

The statistical data analysis followed the schema described for Experiment 1.

RESULTS

Warm-up Trials

Type 1 for the hiding task. The group performance averaged 84% correct responses ($p < .01$). Three of the monkeys (Ch, Lu and Ol) were individually correct above chance level ($p < .01$, Binomial test, one tailed) indicating that the hiding procedure was understood. The fourth subject (Al), that was presented first with the finding task, became so stressed during the presentation of the finding task that the experiment had to be terminated before the presentation of the warm up trials for the hiding task.

Type 1 for the finding task. The monkeys were given on average

25 visible baiting trials with two baits (range=21-30) before the administration of two Warm-up 1 trials. The averaged percentage of correct searches was 95.2% (range=90%-100%). The percentage of correct searches of all the subjects was above chance level ($p < .01$, Binomial test with a chance probability of occurrence of a correct search =.25). The combined percentage of correct searches for the two monkeys (Al and Ol) presented with the Warm-up 1 trials was 73% ($p < .01$) and also significantly above chance level ($p < .01$) considered as individuals. The other two monkeys stopped searching after a few failures and the administration of this task was terminated.

Type 2. As for the child sample, preliminary data analyses showed no major differences between the results obtained from the warm-up 2 trials for the hiding task and the Warm-up 2 trials for the finding task. Therefore, the results from the two tasks have been combined. As with children, monkeys were at chance when locating the object, on their first attempt (22% of the trials). They adopted a Systematic mode of search more often than an Asystematic one, although the percentage of occasions in which the subjects were Asystematic is considerable. In fact, 36 searches (50% of the total number of searches) were performed in a Systematic way, while 20 (28%) were Asystematic.

Hiding and finding task

Group performance. Table 2 shows the percentages of appropriate first searches performed by the monkeys the hiding and finding tasks. It can be seen that the percentage of appropriate first searches was above chance level in the hiding task but was not significant in the finding task. This taken together with a selective effect of sub-conditions within each task type, analogous to that found for the children, leads to a major difference between tasks.

In the hiding task the monkeys identified the location of the object after a first appropriate choice, as shown in Table 2. Successful second searches were above chance level either when following a first appropriate choice at an end point or at an inner point of the array. As shown in table 2, in the finding task, the combined percentage of successful second searches for the two conditions is again above chance level; when analysed according to first search location, second successful searches following an end point first choice are highly significant; those that followed a first choice to an inner location, whilst successful in all cases (3) are too few to yield to statistical test.

Table 2. Distribution of monkey's searches in the hiding and finding tasks. Abbreviations as in Table 1.

Task	Appropriate first searches (%)			First search outcome (%)		Successful second searches (%)		
	All	OP	OA	Object found	Object not found	All	FI	FE
Hiding	87**	93**	81**	54	46	94**	88**	100**
Finding	53	41	65	73	27	100**	100	100**

Individual Performances. As for children, given the asymmetrical distribution of first choices across tasks and conditions, the data were analysed on an individual basis.

In the hiding task, three subjects searched appropriately above chance level in the Object Present condition and two in the Object Absent condition. Neither of the subjects presented with the finding task performed above chance in either the OP nor in the OA condition. Combining the results obtained from the two conditions of each of the tasks secures the conclusion that all three monkeys tested in the hiding task appropriately performed first searches above chance level. In contrast, the two that were presented with the finding task both failed. The main differences are therefore between tasks, not conditions. What seems clear is that the finding procedure is itself difficult to understand. In fact, the subject that was presented with the finding task first never solved it, and expressed distress by moving frantically in the cage and occasionally shaking the apparatus, therefore we were forced to discontinue testing. Moreover, the two subjects that proved successful on the hiding task, failed the warm-up trials of the finding task. After a few unsuccessful attempts they eventually ceased search for the hidden bait.

Identification of strategic behaviours

We have already seen that monkeys behaviour was "logical" while performing the hiding task. However, when presented with the finding task they used a spatial strategy. In particular each subject in the finding task chose always the same end location on the same side (one subject chose left, the other right).

DISCUSSION

Monkeys in this experiment appear able to use the behaviour of a third party in the hiding but not the finding task. This indicates that even in this small task domain, the cost functions are appropriate to the induction of an observationally based strategy. Special, desirable food may well be a strong factor, energising the subject in circumstances where children may need strong social facilitation to maintain attention and devise more complex solutions perhaps than the task may otherwise warrant.

However, where the tester acts as finder, the monkeys fail. While this may indeed be a direct result of a failure to appreciate a "finding" role, as described by Fischer & Jennings (1981) and Berthenthal & Fischer (1983), the fact that the performance of children in our own study was also relatively poor (as indeed was the performance of subjects in the Somerville and Capuani-Schumaker study) indicates that the task is difficult to comprehend. One index of this is given by the number of verbal prompts required in the Somerville and Capuani-Shumaker study (1984). Task communication apart, however, the subject must link some background knowledge with the perception of object displacement i.e. it is crucial that the subject interprets the object event at the end of the finding sequence in the light of the background knowledge that the objects are always together. The most likely reason for the failures in the finding task, therefore, would thus appear to be based on a failure to understand that both items are "always together". If so, there is no reason to believe that a common strategy will operate in the variety of conditions to which the subject is exposed in this experiment. The various task requirements, in fact, scale according to an abductive inference¹ analysis which indicate that each of the conditions of the experiment varies in the demands it makes on the subject. On that basis, we would expect the data to assort according to the hierarchy of difficulty suggested by the analysis. For the same reasons, we would not expect to find any consistency of "strategy" across tasks and conditions, nor do we.

¹ If, as Peirce (1955) suggests (see Luger and Stern, 1990), the observation and identification of facts is conditioned by a background of expectations, than a signal absent condition will frequently demand more of the subject by way of interpretation, than the signal or event on which that interpretation is based. So the partiality of the success, whilst initially paradoxical when the cross over effects due to the object presence/absence as a function of tasks are considered, is quite rational when considered from this perspective.

GENERAL DISCUSSION

A first implication of our results is that capuchins are able, at least under some testing conditions (e.g. the hiding task), to successfully deal with a series of invisible displacements. These results somehow complement studies conducted within the piagetian framework and support results showing a capuchin monkey solving a test for stage 6 of object permanence (Schino, Spinozzi & Berlinguer, 1990) in contrast to another study where all the subjects tested failed (Natale & Antinucci, 1989). However, the fact that also 4 and half year old children failed to solve all conditions of the tasks suggests that the requisite of object permanence was only a component of the skills required for success in the tasks employed here. Although our results provide some information about the controversial issue of the achievement of stage 6 of object permanence in capuchins we would invite caution in reading our results in that light. The tasks we describe in this paper were not specifically designed to evaluate piagetian stage 6 of object permanence in capuchin monkeys. Moreover, it is a long time since it has been indicated that the concept of object permanence might itself conceal a compound of different sub-competencies (Bower, 1974).

The tasks we used have been designed to evaluate the strategies subjects may use when searching for unseen objects. Ostensibly they are about the ways in which the agent constrains search both on the basis of information received and (as in the finding task) on the basis of prior information, needed to interpret the events under the subject's interrogation. The results vary both across and within species. In the former case, the variation seems to have something to do with the type of task used, the effort of searching and the cost functions attaching to that search (see Wellman et al., 1979). In addition, there may well be social factors at work. The (social) costs of mistake in situations where the adult tested has carefully coached the child in the rubric of the test may well contribute to the performance recorded by Somerville and Capuani-Schumaker (1984). Whilst these are unlikely to apply in the case of the monkey, failure to retrieve highly preferred food, albeit in situations where search is otherwise un-costly may dispose the *Cebus* in our experiments to pay particularly good attention to the behaviour of the tester. A further social factor is the sort of role assigned the tester, as hider or as finder, as collaborator or as deceiver. These latter factors may all play a part, particularly in encounters with conspecifics. For these reasons, it may be best to specialise and develop experimental paradigms which target a cohort of closely related issues. For example, the social aspects of the encounters are already represented in

experiments on social inference and imitation. In non-human primates, recent studies by Visalberghi & Frigaszy (1990) and by Povinelli, Parks and Novak (1991) are examples of controlled assessments of the use of socially derived information by non-human subjects.

A complementary but separable line of inquiry is one concerned with self-directed search under conditions which do not presume socially based observational competencies as a precondition for its operation. Here the tasks used in the study we describe are flawed, when considered from this perspective alone. One major reason for this is that each manual interrogation of an object displaces it from its test position, thus leaving a visible trace of a visit. Under these circumstances, it would be a very foolish subject who attempted to reiterate visits to previously interrogated locations. Yet a measure of reiteration is essential if we are properly to evaluate the extent to which subjects can keep track of choices made serially over time.

Recently, serial-order search tasks for human and non-human primates have been developed using paradigms and procedures designed to evaluate size seriation skills (McGonigle, 1987; Chalmers and McGonigle, 1997). These are intended primarily to evaluate self-directed search strategies without reference to a third party. Recently, we have reason to believe that the non-human primate, *Cebus apella* can devise its own strategies in an exhaustive search task, becoming more economical by paying attention to the spatial organisation of items in the search space (McGonigle & Chalmers, 1992, 1996; De Lillo, Visalberghi & Aversano, 1996). As a consequence of this, we will shortly report the results of new paradigms based on computer-interactive touch screen technology which enables the experimenter to display a wide range of items through which the subject must search (for an outline of the paradigms and preliminary results see Terrace & McGonigle, 1994; Visalberghi & De Lillo, 1995; De Lillo, 1997; and McGonigle & Chalmers, 1998). However, unlike our present procedures, each touch leaves no lasting trace of a touch, leaves the subject to discover its own best (most efficient) route through the search space, and is sufficiently motivating to keep the subject working for protracted periods thus enabling a comprehensive in-depth analysis of each case. Apparatus and procedures which satisfy these requirements have also been developed for the study of search skills in environments of larger scale than a computer monitor and used to test capuchin monkeys faced with a variety of different spatial configurations of baited sites (Visalberghi & De Lillo, 1995).

In short, the partitioning of research into issues concerning social

regulatory factors in cognition on the one hand, and self-regulatory ones on the other, offers, we believe, the best prospect for the study of information organisation and management by primates for some time to come.

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BRAIN DIMORPHISMS AND SEX: A REVIEW

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ABSTRACT: In this article we review evidence from studies of fish, amphibians, reptiles, birds and mammals which bears on the question of whether differences in sexual behaviour are reflected by differences in central nervous system (CNS) structure. Neural structures in fish demonstrate the existence of both inter- and intra-sexual dimorphisms related to dimorphic behaviours, as well as environmentally triggered changes in the size of neural structures. Seasonal changes in neural structure in amphibians have demonstrated a strong correlation between sexually dimorphic brain structures and sex-specific behaviours. While in reptiles there are some examples of sexually dimorphic CNS structures, *C.uniparens* demonstrates that differences in brain morphology are not necessary to display sexually distinct behaviour. Birds demonstrate the clearest sex related brain-behaviour differences; the song control nuclei exhibit substantial differences in size between the sexes varying in magnitude in relation to the amount of sexual dimorphism in song production. There are sexually dimorphic areas in the mammalian brain, in areas associated with sexual and maternal behaviour, which are correlated with differences in hormonal environments during ontogeny. No single phyletic trend is obvious, though this could be the consequence of a small number of taxa examined or the different aims of the studies. It appears that sexuality has not necessarily evolved linearly from a particular primitive vertebrate ancestor but is manifested variously in different vertebrate classes, most likely as the result of distinct environmental pressures.

INTRODUCTION

Debate as to whether gender differences are socially constructed or biologically ordained is far from resolved. Following the publication of Margaret Mead's *Sex and Temperament* (1935), the prevailing view

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was that cultural factors and early experiences served to define gender. More recently, especially with the development of the Gay Rights movement in the United States, biological factors have been seen as prominent (LeVay, 1996).

The issue is further complicated by the suspicion that sex is not a bipolar phenomenon, a matter of being either totally male or female. The usual attributes of one's sex, viz. genitals, gonads, karyotype, predominate hormones, etc., may be discordant, suggesting that sex may need to be viewed as having a number of different dimensions. The practical problems this can pose are illustrated by the dilemma of Olympic officials at the 1976 games who were faced with cases of putative female athletes with XY karyotype in their hair cells (reviewed in Klopfer, 1982).

We review evidence that bears on the question of whether differences in sexual behavior are reflected by differences in the structure of particular areas in the central nervous system, or whether brain dimorphisms map onto some other attribute of sex. We also consider whether the dimorphic structures are the cause or the effect of differences in sexual behavior. We examine studies of fish, amphibians, reptiles, birds, and mammals.

FISH

Structural dimorphisms

Neural structures in fish demonstrate the existence of both inter- and intra-sexual dimorphisms. For example the plainfin midshipman, *Porichthys notatus*, has two different male morphs - Type I and Type II, which not only present with distinct sexual behaviors, but also underlying dimorphic neural structures. Type I males are larger than Type II males and represent about 90% of the reproductively active male population (Bass, 1992). While the Type I males build nests and guard their eggs, the Type II males "sneak-spawn" leaving the protective responsibilities to their larger male counterparts (Bass & Marchaterre, 1989; Brantley & Bass, 1991). Despite their smaller body size, Type II males' ratio of gonad size to body size is nine times greater than that of Type I males (Bass & Anderson, 1991). This ratio in females is fifteen times greater than in Type I males.

The vocal behavior of the plainfin midshipman is also dimorphic. While all three morphs generate grunting sounds, Type I males' grunts

are louder and more rhythmic in aggressive situations (Brantley & Bass, 1991). Type I males also generate a hum, a sound of higher amplitude and longer duration than a grunt. This hum is used to attract gravid females to their nest (Brantley & Bass, 1991). Electrical stimulation can cause females to produce sound. The only difference in the electrically stimulated sounds generated by the three morphs is a 20% higher frequency in the Type I male (Bass & Baker, 1990).

The acoustic systems responsible for these dimorphic vocalizations provide an ideal basis for examining the relationship between behavior and neural differences (Bass, 1989). Sonic muscles (SM) attached to each lateral face of the swimbladder contract to produce both hums and grunts (Bass & Baker, 1990). SM's receive input from pacemaker neurons in the brain, via sonic nerves, and together they regulate firing frequency. Each sonic nerve which innervates a SM is a fusion of two occipital nerve roots which exit the brain laterally; these roots originate in the sonic motor nucleus (Bass & Baker, 1990). The vocal control system is anatomically similar in females and Type II males, both of which are less developed than in Type I males. The Type I males' SM mass is six times larger than that of Type II males and females (correcting for body size) (Bass & Marchaterre, 1989; Brantley & Bass, 1991). Additionally Type I males have larger muscle fiber number, diameter, and proportion of myofibers to myofibrils (Bass & Marchaterre, 1989).

More pertinent to the discussion are inter- and intra- sexual dimorphisms in the sonic and pacemaker neurons (Bass & Baker, 1990). Both average diameter of somata and primary dendrites of the sonic motoneurons are significantly larger in Type I males than in females and Type II males. Pacemaker cells also have a larger average soma and dendrite size in Type I males than in females. The ratio of soma diameter, however, to average diameter of the dendrites is not significantly different among the three morphs. This suggests that both the sonic and pacemaker neurons in Type I males are larger but equally scaled versions of those found in Type II males and females (Bass & Baker, 1990).

Functional dimorphisms

Sexual brain dimorphisms in fish also consist of differential neurosecretory activity, including brain peptides such as Substance P and galanin. (Weld & Maler, 1992; Cornbrooks & Parsons, 1991). The dimorphic distribution of these peptides is thought to play a key role in

different reproductive behaviors. However it should be noted that, for most studies cited throughout this review, staining methodology does not differentiate between neurons which actually secrete a particular neuropeptide and neurons which may have a high accumulation of that neuropeptide.

Weakly electric fish generate sexually dimorphic electric organ discharges (EODs) as a means of courtship, territorial, electrolocation, and communication signals. The EODs they produce are of either pulse-type, which are made of brief, irregular rhythmic pulses, or wave-type, which consist of longer duration and very regularly rhythmic pulses (Bullock & Heiligenberg, 1986). Courtship EODs are sexually dimorphic. Female EODs, in pulse fish, are of shorter duration than males (Bullock & Heiligenberg, 1986; Hagedorn & Heiligenberg, 1986). Some female fish, that communicate with wave-type EODs, have discharges of greater frequency and shorter duration than males. Other fish show the reverse pattern (Bullock & Heiligenberg, 1985).

The EOD is controlled by a midline medullary pacemaker nucleus, which receives primary input from the prepacemaker nucleus (PPN) (Kawasaki, Male, Rose & Heiligenberg, 1988). The PPN determines transient changes in EOD frequency called "chirps" in Gymnotiforms (Kawasaki et al., 1988). Weld & Maler (1992) found that Substance P-like immunoreactivity (Spli) was differentially distributed in the PPN between males and females. Dimorphic Spli innervation of this diencephalic cell group arises in either the hypothalamus lateralis (Hl) or the hypothalamus ventralis (Hv). Male Gymnotiforms have more abundant Spli cell bodies and fibers in the Hl, and the Hv was intensely stained in males while devoid of Spli in females (Weld & Maler, 1992). Additionally, Spli distribution is sexually dimorphic in some hypothalamic and septal nuclei. These results suggest that a tachykinin may play an important role in the regulation of sexual differences in fish behavior, EODs (Weld & Maler, 1992).

The male sailfin molly, *Poecilia latipinna*, possesses a sexually dimorphic galanin-like immunoreactivity (GAL-LI) fiber system in the brain extending from mesencephalic levels to caudal structures of the spinal cord (Cornbrooks & Parsons, 1991). The optic tectum, torus semicircularis, brainstem tegmentum, and spinal cord contain higher GAL-Li levels in the male molly than the female (Cornbrooks & Parsons, 1991). Comparative studies looked at GAL-LI distribution in the spinal cord of the goldfish and neonatal mollies, which revealed no sexual dimorphisms. In fact neonatal mollies lacked spinal GAL-LI completely. Thus this unique sexually dimorphic distribution of GAL-

LI, as well as the extensive fiber network present only in the adult male, suggest a role for galanin in sexually dimorphic behavioral displays (Cornbrooks & Parsons, 1991).

Brain-behaviour relationships

Fish display a sexually dimorphic distribution of gonadotropin-releasing hormone (GnRH) cells throughout the brain (Grober & Bass, 1991). This sex difference is related to dimorphic reproductive behaviour in various fish, including sex and role changing fish. In certain species, individuals differentiate as one sex and then change sex later in life. Fish which undergo sex change are called sequential hermaphrodites, of which there are two patterns - protogyny and protandry (Shapiro, 1994). Protogynous species include individuals which change from female to male, whereas individuals in protandric species change from male to female. In these species, changes in reproductive behaviour correlates with the number of GnRH releasing cells within the brain (Grober & Bass, 1991; Shapiro, 1994).

Sex change in fish is manifested in changes in gonad type, external appearance (coloration), and behaviour. The latter two characteristics are secondary sex characteristics, dependent on androgens (Shapiro, 1994). Sex and role reversal is correlated with a change in brain structure, the distribution of GnRH releasing cells, resulting in the altered release of gonadotropin releasing hormone from the brain. Increased gonadotropin levels caused by increases in GnRH are thought to induce sex change. Experiments with human chorionic gonadotropin (HCG), show that this hormone causes females to change in colour and gonad type (Koulisch & Kramer, 1989). Gonadotropin levels are regulated by interactions involving the hypothalamus, pituitary, and gonads. Thus sex change is most likely an example of a sexually dimorphic neuroendocrine feedback loop controlling the secretion of gonadotropins.

Exogenous factors have been shown to influence the development of structural dimorphisms. In Davis and Fernald's studies (1990) on the African chichlid fish, *Haplochromis burtoni*, maturation of males is strongly influenced by the growth of gonadotropin releasing hormone releasing (GnRH-ir) preoptic neurons. Further the growth of the neurons is partially determined by the social environment; no neuronal growth took place when fish were housed in an environment that encourages aggression. This inhibition of neuronal growth appeared to stunt sexual maturation. Growth of neurons and sexual maturation

occurred only when these fish were housed with other fish their age, as opposed to older fish, a presumably less aggressive environment. Thus the fish's social environment affects neuron size which in turn affects the fish's sexual maturation.

In further studies with this species, territorial males were found to have larger gonadotropin releasing hormone (GnRH) releasing neurons in the preoptic area than non-territorial males. A change from territorial to non-territorial status resulted in a reduction of GnRH-ir neurons, whereas a change from non-territorial to territorial status resulted in an expansion (Francis, Soma & Fernald, 1993).

Steroid hormones have been shown to change both the EOD and physiology of the electric organ in several species which demonstrate a sexually dimorphic EOD in the field (Meyer & Zakon, 1982). Landsman, Harding, Moller, and Thomas (1990) performed a study examining the effects of implanted testosterone, dihydrotestosterone and estradiol on EODs and morphology of the weakly electric fish, *Gnathonemus petersii*. They found androgens significantly increased the duration of phases 2 and 3 of the juvenile and adult EOD, and decreased the peak power spectrum frequency (PPSF) of the Fourier transformation (Landsman, et al. 1990). Additionally, androgen induced the male-like indentation of the dorsal margin of the anal fin in juveniles and females (Landsman, et al. 1990). The findings of lengthened EOD duration and decreased PPSF are congruent with seasonal sex differences in the *G. petersii*. These effects were androgen specific and did not occur in individuals implanted with estradiol; estradiol induced a slight increase in PPSFs of adults. Estrogen has been demonstrated in previous studies to influence the PPSFs of other weakly electric fish (Meyer, 1983).

Like the plainfin midshipman, there are two male morphs in the bluehead wrasse - primary and terminal (or secondary males). Sex reversal also occurs in the bluehead wrasse. Grober and Bass (1991) found that luteinizing hormone releasing hormone (LHRH) secreting cells were distributed diffusely in the brains of all three morphs (female, primary male, and terminal male). Although no qualitative differences were found, there were quantitative differences in distribution in the preoptic area and the hypothalamus between the three sexual phases. Terminal males have a significantly greater number of LHRH preoptic cells (2-3 times greater) than primary phase males and females (Grober & Bass, 1991). Grober, Jackson and Bass (1991) found 11-ketotestosterone induced increases in both female and primary male LHRH preoptic cell numbers to levels equivalent to terminal

males. However, 11-ketotestosterone had no effect on terminal phase males, suggesting that these individuals may have reached an end stage in developmental maturity.

This brain dimorphism in LHRH preoptic cell number corresponds with different reproductive strategies. Both primary and terminal males release sperm as females release eggs at the top of the water column (Shapiro, 1994). Terminal males, however, spawn with single females, while primary males spawn in groups of 5 to 40 males for every female (Shapiro, 1994). Shapiro (1994) hypothesizes that the LHRH cell number is more strongly correlated with the development of alternative male reproductive behaviors than with the process of sex change or reversal.

Gonadotropin releasing hormone immunoreactive (GnRH-ir) cells in the preoptic area (POA) of the plainfin midshipman demonstrate differences in cell size rather than cell number as a key component in sexual differentiation, though changes in both occur during development (Grober, Fox, Laughlin, & Bass, 1994). In the Type II morph, the ratio of GnRH-ir cell number increase relative to body size increase is disproportionately greater than in the other two morphs. Grober *et al.* (1994) suggest that the increases, which vary among the three morphs, are reflective of differences in the onset of sexual maturation. Gonadotropin releasing hormone cells in the terminal nerve (TN) and POA appear to play a role in the development and maintenance of teleost sexual behavior (Grober *et al.*, 1994). Significant differences in GnRH-ir cell size in the POA were found among all 3 adult morphs. Sex differences in GnRH-ir cell size nor cell number, however, were found in the TN. The differential timing of POA developmental changes may be a strategy for providing alternative male reproductive morphs.

Dimorphic sexual behaviors have been linked with both functional and structural dimorphisms in the brains of certain fish. In these fish there are often two male morphs, in addition to a female morph, and structural dimorphisms are related to behavior more than the condition of being male or female. Additionally, exogenous factors, such as living environment, can affect the size of neural structures and must also be considered in determining brain-behavior relationships. The causal nexus remains unclear between brain dimorphisms and behavioral displays.

AMPHIBIANS

Structural dimorphisms

Amphibians display sexually dimorphic behaviors which have been correlated with sex differences in both neural structures and circulating levels of hormones or neuropeptides. The clearest and most studied example is the sexually dimorphic anuran mating call. The African clawed frog, *Xenopus laevis*, produces three distinct vocalizations: the mate call, a repetitive trill composed of brief clicks, used by males to attract females; ticking, a slower trill of clicks, used by sexually unreceptive females when clasped; and sawing, an aggressive signal, used by paired sexually active males or androgen-treated females (Kelly, 1986). Male mate calls are acoustically distinguishable from female ticking.

Mate calls and ticking are produced by contractions of the laryngeal dilator muscles which receive input from motor neurons in cranial nerve nucleus IX-X (n. IX-X) of the caudal medulla (Kelly, 1980). n. IX-X receives afferents from inferior and medius reticular nuclei and from the pretrigeminal nucleus of the dorsal tegmental area of the medulla (DTAM); which in turn, are innervated by the ventrolateral striatum, the preoptic area and postero-central and ventral thalamus (Kelly, 1986). It is not yet clear how these CNS areas function to produce the different anuran vocalizations.

Both the larynx and CNS vocalization pathways are sexually distinct in the African clawed frog. The larynx of males is 2-3 times larger in males than females. This difference results from larger cartilage and muscle mass in males; males have an average of 32,000 muscle fibers while females have only 4,000 fibers (Kelly, 1986). There are also physiological sex differences in laryngeal muscle. Male muscle is made up of mostly fast-twitch, fatigue-resistant fibers; while, female muscle is predominantly slow-twitch fiber with some fast-twitch intermingled (Gray, Sassoon & Kelly, 1985). Projections from the preoptic area to the DTAM and recurrent collaterals from laryngeal motor neurons to DTAM are also dimorphic, with females showing a great reduction in size or complete absence (Weltz et al., 1985 cited in Kelly, 1986).

Kelly, Fenstermaker, Hannigan, & Shih (1988) morphologically categorized n.IX-X neurons in, *Xenopus laevis*, and examined them for sex differences. Multipolar n.IX-X neurons were classified based on somal shape (Type I-triangular, Type II-ovoid, Type III-elongated).

The frequency of different types of n.IX-X neurons and primary dendrites were the same between males and females. However, male n.IX-X neurons had a greater number of higher order dendrites, therefore more total dendritic segments, and the male mean length of the dendritic tree was 2.3 times that found in females (Kelly *et al*, 1988). Only males displayed fifth order branches of Type II and III cells.

As mentioned earlier, the anterior preoptic nucleus (APON) provides input to the DTAM. This area is thought to be a triggering center for male mate calling behavior in anuran species. The APON has been found to be sexually dimorphic in many vertebrate species including the Japanese toad, *Bufo japonicus*. Takami & Urano (1984) tested the hypothesis that the APON was responsible for evoking male mating behavior by comparing nuclear volumes between male and female, and also between post-breeding and hibernating *B. japonicus*. The male APON was 125% larger in hibernating than post-breeding toads, whereas in females it did not fluctuate in size. Additionally, the male APON was significantly larger in male than female animals. The ratio of male to female nuclear volume was 1.39 and 1.25 in hibernating and post-breeding toads, respectively (Takami and Urano, 1984). Similar sex differences were found in the nuclear volume of two morphologically and probably functionally related nuclei, the amygdala subnuclei, Am and Al.

Sexual dimorphisms have also been found in amphibian sensory systems, for example, the vomeronasal system in the red-backed salamander, *Plethodon cinereus*. In salamanders, odorants are received through nasolabial grooves and are delivered to vomeronasal receptors in a process known as nose tapping (Dawley & Crowder, 1995). During the breeding season males may use nose tapping to locate and identify potential mates. Vomeronasal size in *P. cinereus* is correlated with overall body size and sex. Male vomeronasal organs are significantly larger than females throughout the year, and this difference is the result of a greater number of cells per section of vomeronasal epithelium (Dawley & Crowder, 1995). In both sexes the vomeronasal organ is largest in the summer, which most likely corresponds to an increase in organ cells during the prebreeding season.

Functional dimorphisms

The neuropeptide arginine vasotocin (AVT) has been shown to influence sexual behavior in a variety of vertebrates, including

amphibians (Moore & Deviche, 1987). Boyd, Tyler & DeVries (1992) used immunocytochemistry to compare AVT distribution between males and females in the bullfrog, *Rana catesbeiana*. While AVT-immunoreactive cells (AVT-ir) were found diffusely throughout the brain, in both hypothalamic and extrahypothalamic areas, there were clear sexual differences in specific brain areas. Males and females demonstrated sex differences in the amygdala pars lateralis and habenular nucleus, with males having a denser distribution of AVT-ir. Additionally, males had larger AVT-ir cell bodies than females in the suprachiasmatic nucleus. No differences were found in the dorsomedial or ventromedial septum nor in the magnocellular preoptic nucleus.

Brain-behavior relationships

Observations of seasonal changes in neural structure and neuropeptide levels, as well as experimental hormonal manipulations, in amphibians have demonstrated a strong correlation between sexually dimorphic brain structures and sex-specific behaviors. Female African clawed frogs are unable to produce male-typical mating calls, even when administered androgen (Kelly, 1986). It appears that females lack the morphology to produce the repetitive trill involved in the male mating call. When the female laryngeal nerve is stimulated at the rate of a male mate call, only one click is produced as successive stimuli act to maintain tonic tension in the arytenoid discs of the larynx (Kelly, 1986). It may be that sexual dimorphism of the CNS vocal control pathway preserves reproduction in the African clawed frog by preventing females from being able to mimic the male mating call. However, it appears that the female vocal limitation is manifested at least partially in the periphery.

Sexually dimorphic seasonal changes in cell number, perhaps cells containing steroid receptors, suggest a causative role for these structural changes in the production of sex-specific behavior (Takami & Urano, 1984). By comparing post-breeding Japanese toads with hibernating toads, seasonal variations in the volume of the anterior preoptic nucleus (APON) were discovered. Additionally, Takami and Urano (1984) found these seasonal changes in neural structure to precede physiological and behavioral changes in the breeding season. Given that the seasonal changes in the APON were only found in male toads, it is more likely that this area of the brain is involved in male-specific activity, either mate calling exclusively or even encompassing other areas of copulatory behavior.

Similarly, the vomeronasal organ was found to be more highly developed in males and seasonally variable in size (Dawley & Crowder, 1995). While the vomeronasal system is used throughout the year for territorial maintenance, it may be that courtship and mating in the breeding season require a different set of hormone receptors. These authors suggest that seasonal fluctuation in vomeronasal cell number may demonstrate neurogenesis of additional receptors used in mating. Males may require a more sensitive olfactory system for identifying potential mates, such that the sexual dimorphism of the vomeronasal system reflects a structural difference underlying sex differences in sensory ability.

Seasonally breeding amphibians show demonstrable fluctuations in gonadal steroid levels associated with sexual behavior and possibly sex differences in morphology. The red-backed salamander, with its sexually dimorphic vomeronasal organ, is a perfect example. In the summer season when the vomeronasal organs are largest in both sexes males have low androgen levels and high GnRH levels (Dawley & Crowder, 1995). Similarly, females have low estradiol and testosterone levels but high GnRH in summer months (Dawley & Crowder, 1995). These findings might suggest the existence of GnRH regulation of sex differentiation; however, further measurements of circulating hormones are needed to elucidate this relationship.

Functional dimorphisms, such as differences in neurosecretory activity, have also been shown to underlie sex-specific differences in mating behaviors. Arginine vasotocin (AVT) has been shown to influence male sexual behavior. Administration of AVT to male rough-skinned newts, *Taricha granulosa*, stimulates clasping behavior in intact newts and androgen primed castrates; whereas, injections of anti-AVT serum inhibits sexual behaviors (Moore & Miller, 1983). Further, it appears that AVT is acting centrally given that intracranial injections of AVT, at levels that are behaviorally ineffective in the periphery, are sufficient to stimulate sexual behaviors (Deviche, Propper & Moore, 1990). Seasonal changes in AVT also supports its role in the expression of sexual behaviors; irAVT concentrations were found to increase fivefold in the optic tectum in the spring when sexual behaviors are most prevalent in male newts (Zoeller & Moore, 1986). Similarly, infundibulum concentrations of irGnRH in male rough-skinned newts increased from the end of May to mid-June with a concomitant increase in plasma androgen, testis weight, and mating behavior (Deviche et al., 1990). These authors suggest that these neuropeptides might be acting directly or through intermediary hormones at multiple sites, such as sensory and motor pathways, to evoke and organize sexual behavior.

REPTILES

Structural dimorphisms

A substantial amount of the research in reptiles has been done on sex differences in the whiptail lizards (*Cnemidophorus* species) because they consist of both sexually distinct and uni-sexual species. For example, the all-female parthenogenetic species *C. uniparens* is the descendant of two sexually reproducing species, *C. inornatus* and another *C. nemidophorus* species (Densmore, Mortiz, Wright & Brown, 1989 cited to Kingston & Crews, 1994). These parthenogenetic females are capable of displaying both male and female-typical copulatory behavior depending on their hormonal status (Lindzey and Crews, 1988).

There are two primary areas involved in the control of *Cnemidophorus* species' mating behavior: the anterior hypothalamus-preoptic area (AH-POA) responsible for producing male-typical sexual behavior and the ventromedial hypothalamus (VMH) involved in female-typical sexual behavior (Wade, Huang & Crews, 1993). Activation of behavior is hormone dependent. Androgen administration in the AH-POA leads to male behavior in gonadectomized male individuals of either species (Mayo & Crews, 1987 cited in Wade et al., 1993). Likewise, estrogen implants in the VMH of either species leads to female-typical receptivity in females (Wade, Huang & Crews, 1993).

Distinct sexual brain dimorphism has been found only in the adults of the sexually reproducing *C. inornatus*. The anterior hypothalamus-preoptic area (AH-POA) is significantly larger in males while the ventromedial hypothalamus (VMH) is significantly larger in females of this species (Crews, Wade & Wilczynski, 1990). In the parthenogenetic species, *C. uniparens*, all individuals display the female brain plan, and there is not a substantial size change in the two critical areas when these individuals alternate their display of male and female mating behavior (Wade, Huang & Crews, 1993).

Thus, it appears that in the ancestral condition there were distinct sexually dimorphic brain areas involved in copulatory behavior. In the evolution of all-female parthenogens, there was a change to a more economical condition where the default (female) brain plan was able to produce both sex-typical behavior patterns given the correct hormonal environment. Therefore, differences in brain morphology do not necessarily correspond with nor are needed for differences in sexual behavior.

Functional dimorphisms

Arginine vasotocin (AVT) is a hormone which has been studied in a number of different reptiles species to determine its distribution and whether there is a sex difference in the cells which produce this peptide. AVT in nonmammalian vertebrates is similar in location and equivalent in function to the mammalian hormone vasopressin (Acher, 1974). Studies have demonstrated AVT's role in antidiuresis in reptiles, and many other important roles have been proposed for this hormone based on the functions vasopressin controls in mammals (Bons, 1983 according to Smeets, Sevensma and Jonker, 1990). These include: memory processes, passive avoidance behavior, thermoregulation, blood pressure, and uterine contractions (Smeets, Sevensma & Jonker, 1990; Propper, Jones & Lopez, 1992). Additionally, AVT may function extrahypothalamically as a neuro-transmitter (Propper et al., 1992). Given that AVT is involved in sexual behavior it is an important peptide to examine for sex differences in CNS distribution.

Stoll and Voorn (1985) have shown a sexual dimorphism in arginine vasotocin (AVT) cell distribution in the lizard, *Gekko gekko*. Male lizards have significantly higher levels of vasotocin (VT) innervation in the areas of the lateral septum, nucleus sphericus, and periaqueductal gray (Stoll & Voorn, 1985). Sexual dimorphism in VT distribution is similar to that in *Gekko gekko*, in the turtle *Pseudmyscripta elegans* and the snake *Python regius*. The most evident sex differences were found in the lateral septal nucleus and the periaqueductal gray areas, with males having greater VT innervation (Smeets, Sevensma & Jonker, 1990). Additionally, less prominent sexual dimorphism was seen in the ventral region, the lateral habenular nucleus, the ventral tegmental area, and the substantia nigra (Smeets, Sevensma & Jonker, 1990). The lizard, *Anolis carolinensis*, has more AVT-ir staining in males than females; specifically in the sexually dimorphic areas of the lateral, medial, and dorsal cortex (Propper et al., 1992).

Reptiles also exhibit sex differences in the central distribution of other neurochemicals including the neuropeptide Y (NPY) and gonadotropin releasing hormone (GnRH). For example given that the lizard, *Pordarcis hispanica*, is a seasonal breeder with hormonal fluctuations corresponding with sexual activity, many hormones such as NPY have been examined for the existence of sexual dimorphism. Results have shown sex differences in NPY distribution in the lateral septal nucleus (LSN) and the periventricular preoptic nucleus (PPN),

which are accentuated during the reproductive season; females have a greater amount of NPY reactive cells in the LSN whereas males show a greater amount of reactive cells in the PPN (Salom, Font & Martinez-Garcia, 1994). Tsai and Licht looked at GnRH distribution in the turtle, *Trachemys scripta*, they found: chicken-I GnRH and chicken-II GnRH had different distributions, CI-GnRH is most likely responsible for gonadotropin release, and there was a sex difference for the distribution of CI-GnRH with females having a greater concentration in the median eminence (Tsai & Licht, 1993).

Brain-behavior relationships

Many studies assume sexual differences in behavior represent an underlying difference in brain structure. Yet, Wade et al. (1993) found all-female parthenogens were capable of producing both male and female-typical behavior without a change in the size of critical brain areas. While much sexual behavior may indeed be related to differences in the size of brain areas between the sexes, this study alerts us to the fact that morphological changes are not necessary for functional changes (Wade et al., 1993).

Research on such species as the lizard, *Podarcis hispanica*, indicates the importance of controls for different seasonal effects on the size of hormonal-regulated structures. Some of the studies did not explicitly test for the persistence of sexual dimorphism in and out of the breeding season.

Differences in behavior between the sexes may be a result of different levels of circulating hormones (i.e. androgens), which mediate pituitary action rather than due to actual structural differences. Although within the reptilian taxa there are clear examples of sexually dimorphic neural structures, the all-female parthenogen whiptail lizard demonstrates that morphological changes are not necessary for behavioral changes (Wade et al., 1993). Additionally, the sex differences in neuropeptides may result from sex differences in body size, blood volume, and blood flow to specific brain structures.

BIRDS

Structural dimorphisms

The best examples of structural brain dimorphisms linked directly

to sexually dimorphic behavior are found in birds. More specifically, gross morphological sex differences have been found in the song control nuclei of birds of the order Passeriformes (songbirds). The brain areas and neural pathways involved in the learning and production of bird song were first described by Nottebohm and Arnold (1976) in canaries and zebra finches; they have since been clearly delineated in several other species. The main descending pathways for vocalization of song consist of: the ventral hyperstriatum (Hvc), which sends an efferent projection to the robust nucleus of the archistriatum (RA), and the hypoglossal nucleus of the medulla (nXII) which is innervated directly by an RA projection. From there motor signals travel to and control neural output of the syrinx, the avian organ for vocal production. There also is a recursive loop involved in the process of song learning in which area X (a forebrain nucleus in the parolfactory lobe) receives information from the Hvc. These are the brain regions which exhibit substantial differences in size between the sexes, and the sexual dimorphisms vary across species in relation to the degree of sexual dimorphism in song production (Brenowitz, Arnold & Lewin, 1985).

In most songbird species song production is sexually dimorphic, with males singing more than females, however birds of different species fall along a broad continuum. For example, male zebra finches sing in order to attract females and ward off competitive females whereas females do not sing at all (Adkins-Regan & Ascenzi, 1990). Females of this species do not sing even when testosterone propionate is implanted in adults (Adkins-Regan & Ascenzi, 1987). Similarly, male canaries have a complex song repertoire and female canaries do not normally sing. Although female canaries will sometimes sing when isolated from males or treated with testosterone in adulthood (Nottebohm, 1980). In these instances female song is simpler and less frequent.

In both the canary and zebra finch, the Hvc, RA, area X and nXII are significantly larger, have more neurons, larger neuronal somata and longer dendritic processes in males than in females (Nottebohm & Arnold, 1976). There were no such differences in other areas not involved in song production, and the sexual differences in volume were more pronounced in the zebra finch. These two findings suggest that the differences are specific to song area and related to dimorphisms in song production.

On the other hand, canaries are more sexually dimorphic than the bay wren. The bay wren is a tropical species in which both sexes

normally sing in duets. In this species there are no sex differences in song complexity, size of song nuclei or accumulation of steroid hormones by neurons in the song control nuclei (Brenowitz & Arnold, 1985a).

In the closely related Rufus and white wrens, males and females also exhibit song behavior in duets, with females having a less complex song. There was no sex difference observed in the proportion of tritium-testosterone labeled target cells in the higher vocal control center of the magnocellular nucleus of the anterior neostriatum(MAN). No information was given about the size of the song control circuitry (Brenowitz & Arnold, 1985b).

Although most work looking at sexually dimorphic neural structures in birds tends to focus on the song control pathways, additional sex differences in brain structure have been reported. One example involves asymmetry in visual pathways connecting the thalamus to the hyperstriatum in the chicken. The ipsilateral connections from the dorsolateral thalamus to the right hyperstriatum are present, whereas there are few contralateral connections to the left hyperstriatum, prior to day 21 (Rogers & Sink, 1988). This asymmetry, which is generated by asymmetrical light exposure of the embryo's eyes, is sexually dimorphic being more pronounced in males. Males treated with 17 beta-estradiol, 5 days prior to hatching, fail to develop a pronounced asymmetry in the thalamofugal projections (Rogers and Rajendra, 1992). This suggests that the asymmetry is dependent on circulating hormone levels, and the lesser degree of asymmetry in females is the result of higher estradiol levels in females prior to hatching.

Functional dimorphisms

Nitric oxide (NO) is hypothesized to play a role in synaptic plasticity. Given this fact, NO is an interesting compound to study for sex differences in the brain and its relationship to behavioral plasticity in song production. Staining for NADPH-diaphorase, an enzyme used in the synthesis of NO, showed that the proportion of stained cells decreases with development, mostly occurring prior to the auditory song learning phase (Wallhausser-Franke, Collins & Devoogd, 1995). When quantifying results for Area X, in zebra finches, it was found that males have a larger decrease in staining (56%) than females (23%) (Wallhausser-Franke et al., 1995). Additional sexual dimorphisms were found in the song control nuclei of adults, with male finches

having a lesser degree of staining in area X, the HVC and RA compared to females. This suggests that NO is more likely involved in early formation of song control circuitry than plasticity needed for song acquisition.

Development, organization, and activation of the song control system are influenced by steroid sex hormones. For this reason the accumulation of sex steroids in song control nuclei has been studied carefully. In canaries, using autoradiographic analysis of injected tritium-labeled testosterone (T), it was found that males and females have equal proportions of cells labeled by T or its metabolites in the four song control nuclei: HVC, MAN, RA, and nXII (Brenowitz & Arnold, 1992). Because males have larger HVC and RA than females, they have a greater absolute number of hormone-sensitive cells in these areas.

The pattern of hormone accumulation in canaries is similar to that of duetting bay wren, rufus, and white wren species which show no sex difference in the proportion of T labeled cells in the HVC or MAN. In contrast, zebra finches show a pronounced sex difference in T labeled cells in the HVC and MAN. This sex difference may reflect more pronounced development of efferent projections from HVC to both RA and Area X in males of the zebra finch species (Brenowitz & Arnold, 1992). Comparison amongst the preceding species suggests that song production can only occur if a sufficient percentage of neurons in song nuclei are hormone sensitive.

Brain-behavior relationships

Experimental hormone manipulation during early post hatching and/or in adulthood has been used extensively to study the effects of sex steroid hormones on the song control nuclei and singing behavior. For example female zebra finches treated with androgens in adulthood show neither changes in singing nor size of song control nuclei. Similarly castrated adult zebra finches, while showing a reduction in song, do not show a reduction in size of the song control circuitry (Adkins-Regan & Ascenzi, 1987). Thus hormonal activation in adulthood is not sufficient to produce singing or the sex differences in song nuclei. It appears that the sexually dimorphic neural circuitry for song is organized early in development and activated in adulthood by testosterone acting on the male-typical structure (Gurney & Konishi, 1980). Female zebra finches injected with estradiol post-hatching and given testosterone as adults, not only sang but also had RA and Hvc

sizes close to those of untreated males (Gurney & Konishi, 1980).

Adkins-Regan *et al* (1994), in studying the influential time for estrogen in the alteration of neuroanatomy and sexually dimorphic behaviors in the zebra finch, found that the first week post-hatching was the critical period for sexual differentiation. Females given estradiol benzoate (EB) during post-hatching week 1 were masculinized in terms of RA neuron soma size and density and dancing behavior, and were partially masculinized with respect to song nuclei size and singing. Males injected with EB during this time failed to mount. Thus both masculinization of females and demasculinization of males is possible during post-hatching week 1.

Nottebohm (1980) demonstrated that testosterone administration to canaries in adulthood can change both neural structures and behavior. Testosterone administered to adult gonadectomized females induced a 90% and 53% increase in size of the HVC and RA, respectively, as these birds acquired male-typical song. These results were similar in magnitude and opposite in direction to the reduction of HVC and RA volumes of males castrated during days 5-10 post-hatching.

Kirn and DeVoogd (1989) suggest that cell death plays a prominent role in the development of structural brain dimorphisms in birds. They examined rates of posthatch neurogenesis and cell death in the vocal control regions - HVC, RA and Area X of the zebra finch. Although the time course for these three areas differed, there were significantly higher numbers of pyknotic, degenerating cells, observed in the Hvc, RA and Area X for females compared to males. Peak levels of cell death occurred 4-6 weeks after hatching, after the onset of sex differences in steroid levels (Kirn & DeVoogd, 1989). Comparisons of cell death and cell incorporation suggest that adult sex differences may result from differential survival of neurons after hatching rather than differential proliferation.

Finally some bird species, including canaries, have been shown to have seasonal changes in brain area sizes that are correlated with behavioral changes. The HVC and RA of adult male canaries are 99% and 76% larger, respectively, in the spring than the fall (Nottebohm, 1981). When the photoperiod increases in spring, the testes grow and secrete androgens, the HVC and the RA double in size, singing increases, and the song repertoire enlarges (Nottebohm, 1981). This author suggests that the changes in song control areas reflect fluctuations in the number of synapses and this underlies the ability to acquire new motor coordinations, thus a structural change preceding a behavioral change.

MAMMALS

Structural dimorphisms

Sex related differences in brain structures are known in several mammalian taxa but have been most studied in rodents and carnivores. The areas of the brain with the greatest number of sexual dimorphisms are the hypothalamus and olfactory system. The vomeronasal system (VNS) is a highly sensitive, sexually dimorphic, olfactory pathway implicated in the control of reproductive behavior (Collado, Valencia, Del Abril, Rodriguez-Zafra, Perez-Laso, Segovia & Guillamon, 1993). The accessory olfactory bulb (AOB) is the first target of vomeronasal input from the vomeronasal organ. The rat AOB is sexually dimorphic: males have greater AOB volume, more mitral cells, and more light and dark granule cells than females (Perez-Laso, Valencia, Rodriguez-Zafra, Cales, Guillamon & Segovia, 1994). These sex differences appear to arise postnatally as a result of the hormonal environment.

The bed nucleus of the accessory olfactory tract (BAOT) is a forebrain group of cells which receives vomeronasal input from the AOB and sends efferents back to the AOB and medial preoptic area (MPA). The BAOT is involved in the control of reproductive and parental behavior (Collado et al., 1993). Male rats have greater BAOT volumes, number of neurons, and neuron to glia ratios than females.

The bed nucleus of the stria terminalis (BST) is a forebrain structure which connects olfactory nuclei with components of the amygdaloid complex, and is considered to be a secondary olfactory center (Segovia & Guillamon, 1993). Some of the divisions of the BST are sexually dimorphic. The medial division, posterior part (BSTMP) has a larger volume and more neurons in male rats than in females (Segovia & Guillamon, 1993). Analogous sex differences have been found in the guinea pig. Conversely the medial division, anterior part (BSTMA) showed a larger volume and greater number of neurons in female rats compared to males.

The medial preoptic area (MPA) receives olfactory input from the BSTMA and BSTMP by way of the stria terminalis. The MPA is involved in many behaviors including: maternal behavior, male and female copulatory behavior, and the cyclic release of gonadotropin in females (Segovia & Guillamon, 1993). Dorner and Staudt (1969, cited in Segovia & Guillamon, 1993) found that female rats presented a larger nuclear volume of the medial preoptic area-anterior hypothalamus continuum than males. Gorski et al. (1980) found a

group of cells in the male MPA that had higher staining than in female rats and named it the sexually dimorphic nucleus of the preoptic area (SDN-POA). This nucleus is 2.6 times larger, contains larger neurons, and displays greater neuronal density in males (Segovia & Guillamon, 1993). Female ferrets entirely lack a sexually dimorphic structure in the MPA, the male nucleus of the preoptic/anterior hypothalamic area (MN-POA/AH) (Cherry & Baum, 1990).

Other dimorphisms include the numerical densities in spine and shaft synapses in the Ventromedial nucleus (VMN) of the rat, which are higher in adult males than females (Miller & Aoki, 1991). This sexual dimorphism was evident by day 5 and persisted into adulthood.

Sex differences have also been found in two hypothalamic nuclei that receive vomeronasal input: the ventromedial hypothalamic nucleus (VMH) involved in feminine reproductive behavior and the premammillary nucleus, ventral part (PMV) which is a tonic center for gonadotropin secretion (Segovia & Guillamon, 1993). Female rats have larger VMH nuclei than males, while the volume of the VMH is significantly larger in males (Matsumoto & Arai, 1983). The size of the nuclei of PMV neurons is larger in male rats than females.

A final CNS structural dimorphism to consider involves a set of spinal motoneurons that innervate the muscles attached to the base of the rat penis. This group of neurons, is collectively named the spinal nucleus of the bulbocavernosus (SNB). These neurons control the muscle groups responsible for the external anal sphincter and penile erection. Adult male rats have a larger SNB which contains more motoneurons than females (Breedlove & Arnold, 1983).

Functional dimorphisms

The vasopressin and oxytocin containing nucleus (VON) of the pig hypothalamus exhibits a significant sexual dimorphism in adulthood, with females displaying three times the number of VON neurons and two times as large a VON area (Van Eerdenburg & Swaab, 1991). Both sexes show a 2.5 fold increase in neuron number around puberty, but the female VON continues to increase in neuron number between 1 and 2.5 years of age. The function of the VON is yet to be delineated, however, because of the timing in sexual differentiation it is likely involved in reproduction.

Van Eerdenburg also studied the supraoptic nucleus (SON) of the hypothalamus of the pig, an area characterized by large neurons that produce vasotocin or oxytocin. Again a sexual dimorphism was found,

though it did not persist into adulthood. Males showed earlier SON enlargement with a 30% and 50% greater volume than females, at 30 weeks and 1 year respectively (Van Eerdenburg, Lugard-Kok & Swaab, 1992). At two and a half years of age there were no sex differences in SON volume. Unlike the VON, testosterone does not suppress development of the SON and gonadectomy does not lead to an increase in SON volume and cell number.

Sexual differences have also been found in the brain opioid system which has been implicated in the modulation of the hypothalamo-pituitary complex. U-opioid receptors in particular have been implicated in the control of gonadotropin and prolactin release since the density of hypothalamo-pituitary u-opioid receptors in the female rat is higher than that of mature male rat (Limonta, Dondi, Maggi & Piva, 1991). Further it appears that the hormonal environment at birth may dictate the development of this sexual dimorphism. Administration of testosterone to female rats soon after birth leads to an ontogenetic pattern of u-receptors similar to that of males, while early orchidectomy in males presents a maturational process similar to that of normal female rats (Limonta, Dondi, Maggi & Piva, 1991).

Brain-behavior relationships

Sex difference in the mammalian brain arise from different steroid hormones issued from the gonads early in development. Developing males secrete testosterone which enters the blood stream and travels to the brain. Centrally testosterone may be metabolized to estradiol or reduced to dihydrotestosterone and can bind receptors, which in turn bind specific segments of DNA to increase or decrease the expression of genes. These DNA domains may dictate the pattern of development for neural circuits necessary for the production of masculine structures and behavior. Feminine behavior and neural structure results when the masculinizing actions of testosterone do not occur. These developmental processes occur during early critical periods in development (Arnold & Schlinger, 1993).

Many experiments have been done in which orchidectomy and hormonal manipulations have been used to test the reversibility and stability of sexually dimorphic neural structures, and their relationship to sex-specific behaviors. For example gonadectomized adult male rats, with AOB bilateral lesions, will perform the female receptive position lordosis when primed with estradiol-progesterone; whereas, gonadectomized estradiol primed males with intact AOBs will not

(Segovia & Guillamon, 1993). This finding suggests that the sexually dimorphic AOB is related to the inhibition of feminine sexual behavior. Similarly bilateral lesions to the sexually dimorphic BAOT facilitates maternal behavior in both female and male rats. Male orchidectomy and female androgenization performed on day 1 can reverse the sexual dimorphism of the BAOT (Segovia & Guillamon, 1993).

There is significant evidence that the GABAa/benzodiazepine receptor Cl⁻ channel complex is involved in the sexual differentiation of vomeronasal structures, such as the AOB, which contain GABA neurons and fibers. It was found that diazepam administered rat pups on post day 0 through 16 lead to decreases in the volume of the AOB mitral cell layer and the number of mitral cells in male rats, while female rats were unaffected (Perez-Laso et al. 1994). These results mimic the effects produced by gonadectomizing the male rat. Diazepam may act by increasing endogenous GABAergic activity, altering Cl⁻ flux and inducing cellular loss in the genetic male (Perez-Laso, et al., 1994). Male rats are more susceptible to diazepam effects; it may be that females have a natural increase in GABAergic activity, regulated by sex steroids, which leads to normal feminization or diazepam might suppress the neurotrophic activity of gonadal steroids on the male AOB (Perez-Laso et al., 1994).

The medial preoptic area (MPA) is involved in reproduction, for example in the display of maternal behavior. Lesions to the MPA after parturition abolishes maternal behavior, while estrogen benzoate implants facilitate it (Numan, 1988). Transplants of MPA tissue from male rats to females induces increases in both masculine and feminine sexual behavior. This at first dichotomous role for the MPA is explained by the fact the MPA has both androgen and estrogen receptors (Segovia & Guillamon, 1993). The sexually dimorphic nucleus of the preoptic area (SDN-POA) also seems to be involved in the control of sexual behavior. In sexually naive males, bilateral lesions to the SDN-POA decreased the number of animals ejaculating, and/or increased latencies to the first mount, intromission, and ejaculation (Segovia and Guillamon, 1993).

The volume of the SDN-POA can be influenced by the hormonal environment perinatally. Castration of a 1 day old male rat will significantly reduce the adult size of the SDN-POA (Gorski, Gordon, Shryne & Southam, 1978). Administration of testosterone propionate on day 2 to the feminized male restores the SDN-POA to normal male volume (Jacobson, Csernus, Shryne & Gorski, 1981). Testosterone propionate administered to intact female pups on day 2 or 4 increases

the volume of the SDN-POA in the adult (Gorski et al., 1978). It is believed that testosterone masculinizes the SDN-POA through aromatization of testosterone to estradiol (Rhees, Shryne & Gorski, 1990). Perinatal treatment of females with diethylstilbestrol (DES), a synthetic estrogen, increases the volume of the SDN-POA to that of males (Tarttelin & Gorski, 1988). There is a definite critical period for this masculinization by estradiol; onset of the hormone-sensitive period begins on day 18 of gestation and terminates on post-natal day 5 (Rhees et al., 1990).

The preoptic area-anterior hypothalamus (POA/AH) is a sexually dimorphic region which has been implicated in masculine and feminine sexual behavior. Lesions of this area lead to deficits in masculine sexual performance while implantation of testosterone into this area activates male coital behavior after castration (Cherry & Baum, 1990). Similarly, electrical stimulation of the POA/AH activates sexual response in male rats and opossums. Furthermore, bilateral lesions of the male nucleus of the POA/AH in ferrets are associated with decrements in male sexual behavior, and enhancement of female proceptive behaviors in response to estradiol benzoate (Cherry & Baum, 1990). It appears that the MN-POA/AH functions normally to inhibit female sexual displays.

The amount of social play, a sexually dimorphic behavior in many species, also appears to result from differences in early hormonal environment between the sexes that leads to the differentiation of neural tissue (Meaney, 1988). Adult male Norway rats, *Rattus norvegicus*, engage in more frequent play-fights than females of this species. Exposure to androgens neonatally influences the amount of play-fighting; testosterone given to female neonates leads to masculinization of social play (Goy & Goldfoot, 1974). Given that the sex-difference in play fighting occurs prior to hormonal surges accompanying puberty, it is most likely that testosterone has an organizing effect on the central nervous system. It also appears that the sex difference in social play is a testosterone or DHT effect rather than testosterone-derived estradiol; neonatal administration of flutamide, an anti-androgen, prevents masculinization of play-fighting (Meaney, 1988). The amygdala has been suggested as the sexually dimorphic neural locus for social play. Lesions to the amygdaloid complex on days 21 or 22 reduce the male level of play-fighting to female levels while having no effect on female play-fighting (Meaney, 1988).

The sexually dimorphic spinal nucleus of the bulbocavernosus (SNB) is also very dependent on the neonatal hormonal environment.

Early in fetal development females possess the group of muscles which control penile erection. As these muscles atrophy, however, the SNB regresses in the female. Females treated with androgen are spared the muscle atrophy and secondarily the SNB (Fishman, Chism, Firestone & Breedlove, 1990). It is the muscle cells, not the motoneurons, that contain the androgen receptors which trigger the development of this sexual dimorphism.

Important research has shown that naturally occurring exogenous events may also contribute to the masculinization of the neural system and sexual behavior. For example, male rats receive more perineal stimulation from maternal licking than do female rats. This maternal bias appears to result from the difference in hormonal status of rat pups; Moore, (1982) in an experiment where injections of testosterone, estradiol or dihydrotestosterone were administered on the day of birth to females, found that all three manipulations lead to equivalent amount of maternal licking to males. Later research by Moore (1992) demonstrated that this difference in maternal stimulation leads to some of the dimorphisms between the sexes in nervous system morphology and behavior. Moore(1984) varied maternal licking by interfering with the mothers' olfaction and then gonadectomized and subsequently administered testosterone to both males and females. Male rats which received less maternal licking had longer ejaculatory latencies, longer post-ejaculatory intromission latencies, and longer inter-intromission intervals than controls. Females showed commensurate deficiencies in copulatory timing. This model exemplifies how variations in hormone levels between the sexes may act indirectly to affect behavioral displays rather than directly on the central nervous system.

Related research in rats has shown that infantile handling has an interactive effect with hormone levels in determining the size of the sexually dimorphic corpus callosum. There is marked sexual dimorphism of the rat corpus callosum, with the male corpus callosum being larger than the female and having greater width of the genu and splenium (Berrebi, Fitch, Ralphe, Denenberg, Friedrich & Denenberg, 1988). Handling of rats in infancy enhances these sex differences (Denenberg, Fitch, Schrott, Cowell & Waters, 1991). Female rats handled in infancy and given an injection of testosterone propionate (TP) at Day 4 will have callosa equivalent in size to males while females administered TP without infantile handling, do not develop a larger callosum (Denenberg, et al. 1991). These authors suggest that corticosterone, released during handling, interacts with the organizational effects of TP on the central nervous system. Denenberg

(1981) further hypothesized, in comparing handled and nonhandled male rats, that handling leads to a more lateralized brain observable in a variety of behavioral tests.

There are sexually dimorphic areas in the brain of mammals. These sex differences in neural structure are correlated with differences in hormonal environments during ontogeny, and these dimorphisms can be reversed with appropriate hormonal manipulations early in development. The brain areas with the greatest amount of sex differences have been shown, through lesion studies and hormonal implants, to be intimately involved in sexual and maternal behavior. However, in order to understand the extent to which these dimorphisms influence behavior we must ensure the focus is on the correct behaviors, avoiding the possibility that the neurological structure in question is more tightly tied to some other behavioral display.

CONCLUSIONS

There are undeniably areas in the brain whose structure varies according to the gonadal status or the behavior of the possessor. This is the case in fish, amphibians, reptiles, birds, and mammals. Whether this is also the case in primates is a separate, debatable issue, which we do not address here.

Most of the studies we reviewed left the causal relations unexplored: do particular brain structures dictate particular aspects of sexual behavior, or can the behavior activate feedback processes that lead to changes in brain structure? Examples of both patterns have been found in certain species of fish and birds. In some taxa there is an obvious change in brain structure preceding the demonstration of sex-specific behavior. Other taxa demonstrate behavioral change triggered by environmental events and changes in brain structure followed. Examples were explored where the perinatal hormonal environment, which is ever important in the development of neural structures, acts differently upon genetic males and females, with one sex or the other being more resistant to its effects.

No single phyletic trend is obvious, though this could easily be the consequence of the small number of taxa that have been examined, as well as by the rather different aims of the studies. Bird studies focused on the neural control of the song of males, while fish experiments examined cues that led to behavioral and gonadal changes in sex. Amphibian and reptile studies were concerned primarily with seasonal

changes in behavior and neural structure. Mammalian studies have often had as their primary goal the elucidation of the role of prenatal hormones in the shaping of gonadal and neural structures, with the interactive role of behavior often ignored. However, it is also possible that there is simply no single trend.

While no singular trend was discovered, there were common themes surrounding the nature of sexual dimorphisms throughout many taxa which are a useful focus for further study. The hypothalamus, including areas such as the preoptic, sexually dimorphic and suprachiasmatic nuclei, was the structure most cited as being sexually dimorphic including examples in amphibians, reptiles, birds and mammals. Central and peripheral structures intimately involved in communication were significantly different between males and females in size and/or composition in fish, amphibians, birds, and mammals. While between taxa the communication system may be as varied as the EODs in fish, song in birds, or odor detection in mammals, all represent ways to send signals between the sexes, often critical for the preservation of reproduction. Similar differences in production or accumulation of analogous hormones involved in the development and maintenance of sex differences in structure or behavior were also found across taxa, including the complicated feedback loop controlling gonadotropin release.

At least two conclusions can be provisionally drawn. First, as with other indicators of sex, such as gonads, karyotype, or genitals, specific brain structures are but one element of the many that define sex. The studies we have reviewed reinforce the view that sex is a multifaceted and complex attribute. Secondly, sexuality has not necessarily evolved linearly from a particular primitive vertebrate ancestor: sexuality is variously manifested in the different classes of vertebrates (cf Short & Balaban, 1994). Thus it is likely that central control mechanisms have multiple origins, reflecting the varied evolutionary strategies required by different species for their reproduction and survival. This is a lesson well known to comparative biologists and psychologists, but perhaps one that others who would use comparative data need to be taught (cf Klopfer, 1996).

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